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Spatial heterogeneity across five rangelands managed with pyric-herbivory

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Summary

1. Many rangelands evolved under an interactive disturbance regime in which grazers respond to the spatial pattern of fire and create a patchy, heterogeneous landscape. Spatially heterogeneous fire and grazing create heterogeneity in vegetation structure at the landscape level (patch contrast) and increase rangeland biodiversity. We analysed five experiments comparing spatially heterogeneous fire treatments to spatially homogeneous fire treatments on grazed rangeland along a precipitation gradient in the North American Great Plains.

2. We predicted that, across the precipitation gradient, management for heterogeneity increases both patch contrast and variance in the composition of plant functional groups. Furthermore, we predicted that patch contrast is positively correlated with variance in plant functional group composition. Because fire spread is important to the fire–grazing interaction, we discuss factors that reduce fire spread and reduce patch contrast despite management for heterogeneity.

3. We compared patch contrast across pastures managed for heterogeneity and pastures managed for homogeneity with a linear mixed-effect (LME) regression model. We used the LME model to partition variation in vegetation structure to each sampled scale so that a higher proportion of variation at the patch scale among pastures managed for heterogeneity indicates patch contrast. To examine the relationship between vegetation structure and plant community composition, we used constrained ordination to measure variation in functional group composition along the vegetation structure gradient. We

used the meta-analytical statistic, Cohen's d, to compare effect sizes for patch contrast and plant functional group composition.

4. Management for heterogeneity increased patch contrast and increased the range of plant functional group composition at three of the five experimental locations.

5. Plant functional group composition varied in proportion to the amount of spatial heterogeneity in vegetation structure on pastures managed for heterogeneity.

6. *Synthesis and applications*. Pyric-herbivory management for heterogeneity created patch contrast in vegetation across a broad range of precipitation and plant community types, provided that fire was the primary driver of grazer site selection. Management for heterogeneity did not universally create patch contrast. Stocking rate and invasive plant species are key regulators of heterogeneity, as they determine the influence of fire on the spatial pattern of fuel, vegetation structure and herbivore patch selection, and therefore also require careful management.

Keywords: Biodiversity conservation, Fire–grazing interaction, Grazing management, Heterogeneity, Patch contrast, Pyric-herbivory, Working landscapes

Introduction

Many rangelands worldwide are working landscapes managed to meet economic goals as well as biological goals (Polasky *et al.* 2005; Ellis & Ramankutty 2008). When economic objectives take precedence, rangeland biodiversity is imperilled, such as when rangeland is converted to cropland or overgrazed by livestock (Samson & Knopf 1994; Fuhlendorf & Engle 2001; O'Connor *et al.* 2010). Moreover, conventional rangeland management promotes spatially-uniform, moderate grazing and the homogeneous removal of biomass by grazers at the pasture scale (Holechek, Pieper, & Herbel 2003) even though uniform moderate grazing degrades habitat quality and contributes to the decline of rangeland biodiversity (Fuhlendorf & Engle 2001; Derner *et al.* 2009).

Many rangelands evolved under patchy disturbance regimes that vary in frequency and intensity across multiple spatial scales (Fuhlendorf & Smeins 1999), therefore, reconciling conservation and agricultural production in rangeland probably depends upon heterogeneity-based management analogous to historical patterns of disturbance (Fuhlendorf & Engle 2001). Heterogeneity is an important driver of biodiversity and an essential component of conservation in ecosystems worldwide (Ostfeld *et al.* 1997). Although heterogeneity consists of many ecosystem attributes, we apply the concept of patch contrast, which describes the degree of difference between patches of otherwise similar properties (Kotliar & Wiens 1990). Patch contrast is a useful concept for rangeland heterogeneity because many rangelands evolved under a shifting mosaic of fire and grazing, in which grazing is concentrated on the most recently-burned portions of the landscape in response to the high-quality forage that grows after fire and focal grazing (Archibald & Bond 2004; Allred, Fuhlendorf, Engle, *et al.* 2011). Patch contrast is created as grazers and vegetation respond to the pattern of fire in the landscape (Adler, Raff, & Lauenroth 2001). This fire–grazing interaction – or pyric-herbivory – is an ecological disturbance that differs from the effects of fire and grazing alone (Fuhlendorf *et al.* 2009).

When applied in a management context as patch burn–grazing, pyric-herbivory supports rangeland biodiversity by increasing the diversity of habitat types, ranging from low stature grazing lawns in recently-burned patches to tall, mature plants in patches unburned for several years (Fuhlendorf & Engle 2004; Winter *et al.* 2012). Such differences in vegetation structure are driven by the pattern of grazing as well as by differential plant responses to the fire–grazing interaction among patches: the relative abundance of plant functional groups varies across patches according to the length of time since a patch was burned (Fuhlendorf *et al.* 2006; Winter *et al.* 2012). Again, patch contrast is a useful term to describe heterogeneity among patches because habitat diversity reflects the degree of difference in vegetation structure among rangeland patches (Fuhlendorf *et al.* 2006; Coppedge *et al.* 2008).

Heterogeneity clearly benefits biodiversity on rangeland, but universal efficacy of the fire-grazing interaction is less clear. We use vegetation structure and plant functional group composition data from five experiments that compare management for heterogeneity (pyric-herbivory) with management for homogeneity (grazing with homogeneous fire regimes).The five experimental locations span several gradients, including precipitation and plant community type and land-use history. Given that evidence supporting an operative fire-grazing interaction has been demonstrated in a breadth of ecosystems worldwide (Allred, Fuhlendorf, Engle, *et al.* 2011), we did not expect the strength of the fire–grazing interaction to vary across the ecological gradient (plant community types and precipitation). However, because invasive species and intense grazing both influence fuel load and continuity, which in turn affect fire spread (Davies et al. 2010; McGranahan et al. 2012), we had reason to believe invasive species and intense grazing might reduce the strength of the fire–grazing interaction.

In this study, we test the following hypotheses using comparable data from five experiments: 1. Patch contrast is greater in rangeland managed for heterogeneity when compared to rangeland managed for homogeneity; 2. Heterogeneity-based management increases variance in the composition of plant functional groups; and 3. Patch contrast is positively correlated with variance in plant functional group composition. We found that patch contrast was associated with variance in plant functional group composition and that management for heterogeneity created variation in vegetation structure. However, management for heterogeneity did not universally create patch contrast across our five study locations. Stocking rate and invasive plant species appear to regulate patch contrast more than primary productivity despite the precipitation gradient and differences in plant communities across our study locations.

Methods

Study locations

To compare the effect of spatially heterogeneous and spatially homogeneous fire regimes on grazed rangeland, we combined vegetation structure and plant functional group composition data from five experimental locations in central North America that span circa 650 km from mixed prairie in the southwest to eastern tallgrass prairie in the northeast (Table 1). The five locations include: Hal and Fern Cooper Wildlife Management Area, Woodward County, Oklahoma; Marvin Klemme Range Research Station, Washita County, Oklahoma; Oklahoma State University Range Research Station, Paine County, Oklahoma; Tallgrass Prairie Preserve, Osage County, Oklahoma; and the Grand River Grasslands, Ringgold County, Iowa. While each experiment was established independently, similarity of experimental design, treatment structure, and data collected provide the opportunity to test for a connection between heterogeneity-based management and actual heterogeneity in vegetation across a broad geographic area.

Data

We used vegetation structure and plant functional group composition data from each of the five locations. Data were similar across all locations. Appendix S1 in Supporting Information includes detailed accounts of the types of data and their specific collection methodologies. At each location, cattle (*Bos taurus*) were stocked continuously during the grazing season on all pastures and cattle were allowed unrestricted access to grazing and water within each pasture, without interior fencing. Across all five locations, vegetation structure was quantified with visual obstruction measurements, which combine vegetation height and vegetation density (Harrell &

Fuhlendorf 2002). Visual obstruction methods used in this study include visual obstruction reading (Robel *et al.* 1970) and angle of obstruction (Kopp *et al.* 1998).

Plant functional group data were collected once each year at each location. Canopy cover estimations follow the Daubenmire (1959) cover class index at all but the Cooper location, where canopy cover was estimated to the nearest five per cent. While sampling periods varied slightly across locations (see Appendix S1), the timing of the sampling periods was consistent from year to year within each location. Sampling at each location followed a nested hierarchical design in which pastures were divided into patches and patches were divided into transects. Sampling points were randomly located along transects to measure visual obstruction and plant functional group canopy cover (sampling points were located within avian point count areas rather than along transects at the Tallgrass Prairie Preserve).

Data analysis

Spatial heterogeneity in vegetation structure.—To compare spatial heterogeneity in vegetation structure (patch contrast) across heterogeneously-managed and homogeneously-managed rangeland, we used a linear mixed-effect (LME) regression model to determine the proportion of variance in vegetation structure attributable to each sampled spatial extent, and compared the average proportion of variance in the patch term across treatments within each location (Winter *et al.* 2012). We created an LME regression model with an intercept-only fixed-effect term (+1) and a random-effect term that included the spatial extents that were sampled in common to each location – sampling point, patch, and pasture – and a year factor to account for repeated measures using the lmer function in the lme4 package for the R statistical environment (Bates & Maechler 2010; R Development Core Team 2011). Because of the hierarchical and annually-repeated design common to all five experiments, the random-effect term for each location was fully crossed to account for statistical interactions between sampled spatial extents and time. Variance estimates were returned for each factor in the random-effect term plus an additional residual error factor (Baayen, Davidson, & Bates 2008). We calculated the proportion of variance contributed by each factor by applying the sum of the variance estimations as a divisor to each factor's original variance estimate. The LME model was applied to each pasture within each location.

We tested for a difference in mean proportion variance in vegetation structure to compare pastures managed for heterogeneity and homogeneity within each location using a Student's t test in the R stats package. A significantly greater proportion of variance in the patch term for pastures managed for heterogeneity within a location indicates that heterogeneity-based management created patch contrast in vegetation structure within these pastures.

Spatial heterogeneity in plant functional group composition.—To test the hypothesis that management for heterogeneity increases variance in plant functional group composition, we first calculated the range of plant functional group composition in constrained ordination space. We specified vegetation structure as the constrained axis in a redundancy analysis (RDA) of plant functional group data for each location, and calculated the range of values, or site scores, along the RDA constrained axis for each pasture. Redundancy analysis is a constrained ordination that calculates variation in multivariate data with respect to *a priori* constraints (Ter Braak 1986; Oksanen *et al.* 2011). This method allowed us to compare variation in plant functional group composition with specific reference to the vegetation structure gradient, specified as RDA axis 1 (RDA1). We used the rda function in the vegan package for the R statistical environment (Oksanen *et al.* 2011).

We scaled RDA1 output to allow the comparison of ordination results across all locations. The overall range of possible variation in each ordination varied by location because a separate ordination was performed for each location, and each ordination was based on the specific plant functional groups measured at each location (see Appendix S1). Thus, prior to further analysis, we combined RDA1 site scores into a single dataset and scaled the data to create a standardized distribution that allows comparison across locations.

The range of site scores for a given pasture along RDA1 represents the variation in plant functional group composition, as pastures with a greater range of functional group composition span a larger range of site scores along RDA1. We tested for a difference in the mean range of RDA1 scores to compare pastures managed for heterogeneity and homogeneity within each location using a Student's t test in the R stats package. Again, a significantly greater range for pastures managed for heterogeneity within a location indicates that heterogeneity-based management created variance in plant functional group composition within these pastures.

Calculating effect sizes.—We used a meta-analytical statistic to compare the effect of heterogeneity-based management on patch contrast and plant functional group composition across all five locations. Effect size statistics use a single value to quantify the difference between two replicated groups by comparing the mean and variance of each group (Harrison 2011). Effect size has been used elsewhere to compare the effect of ecological management across studies testing common hypotheses (Côté & Sutherland 1997). Here, the greater the effect size for a location, the more pronounced the difference between response variables among pastures managed for heterogeneity compared to pastures managed for homogeneity. We calculated the meta-analysis statistic Cohen's d (Cohen 1977) for each response variable, proportion variance and range of RDA1 scores, to determine effect size with the following formula:

$$d = (\mu_{het} - \mu_{hom}) / \sqrt{(\sigma_{mean})},$$

In which μ_{het} and μ_{hom} represent the mean value of the response variables in pastures managed for heterogeneity and homogeneity, respectively, and σ_{mean} represents the mean standard deviation of each response variable. Using the R statistical environment, we estimated 95% confidence intervals with a two-part iterative re-sampling algorithm. First, a sampling distribution for each Cohen's d was generated by 1000 simulations of each treatment groups' mean and standard deviation. Second, the calculated Cohen's d was compared to the generated sample distribution with 9999 iterations at alpha = 0.05 to generate the 95% confidence interval.

To test our third prediction that patch contrast is positively correlated with variance in plant functional group composition, we plotted the patch contrast effect size against the plant community composition effect size and calculated a correlation coefficient using Kendall's T, a non-parametric test for association between two variables based on similarity of rank (Kendall 1938).

Results

Management for heterogeneity increased patch contrast at three of the five experimental locations used in this study (Cooper, Stillwater, and the TGPP) (Fig. 1). At two locations, Klemme and the GRG, management for heterogeneity did not increase spatial heterogeneity in vegetation structure compared to management for homogeneity, and thus did not create patch contrast.

At Klemme and the GRG, variance in vegetation structure among pastures managed for heterogeneity was lower and variance in vegetation structure among pastures managed for homogeneity was higher than at Cooper, Stillwater, and the TGPP. In other words patch-level variation was neither as great as expected on pastures managed for heterogeneity at Klemme and the GRG, nor was patch-level variation as low as expected on pastures managed for homogeneity at these two locations.

Management for heterogeneity increased the variance in plant functional group composition at two of the five locations (Cooper and the TGPP) (Fig. 2). An outlier among pastures managed for homogeneity at Stillwater increased the variation around the mean such that, despite generally higher variance in plant functional group composition among pastures managed with heterogeneity, the difference was not significant (P = 0.08). As above, there was no difference between pastures managed for heterogeneity and those managed for homogeneity at Klemme and the GRG.

Calculated effect sizes for patch contrast and variance in plant functional group composition were positive for both measures at all five locations, but at only three locations (Cooper, Stillwater, and the TGPP) was Cohen's d significantly non-zero based on estimated 95% confidence intervals (Fig. 3). This trend was consistent for both patch contrast and variance in plant functional group composition. In no instance did management for heterogeneity produce a negative effect size in relation to management for homogeneity. The positive association between patch contrast and variance in plant functional group composition (T = 0.40) indicated that the amount of spatial heterogeneity in vegetation structure on pastures managed for heterogeneity generally varied in proportion with plant functional group composition.

Notably, differences in patch contrast and plant functional group composition were associated with neither environmental factors along the geographic gradient, nor with differences in management, including pasture size, number of patches, or fire regime (Table 1). For example, pastures managed for heterogeneity at the most arid location in the mixed-grass prairie (Cooper), and in two of the three mesic, tallgrass prairie locations (Stillwater and TGPP) had significant patch contrast compared to pastures managed for homogeneity. Thus, whether patch contrast followed management for heterogeneity was independent of climate and vegetation type. Likewise, pasture area did not appear to affect whether patch contrast followed management for heterogeneity, as the area of pastures at Stillwater was similar to the area of pastures at Klemme and the GRG. Historical stocking rate, however, was associated with differences in patch contrast: only Klemme and the GRG were stocked heavily prior to the beginning of the experiments (Table 1), and management for heterogeneity at these locations did not create patch contrast compared to management for homogeneity.

Discussion

We found that management for heterogeneity applied through patch-burn grazing increased patch contrast and increased the variance in plant functional group composition at three of the five locations. Overall, patch contrast increased with variance in plant functional group composition. Whether management for heterogeneity created patch contrast was unaffected by precipitation, vegetation type, primary productivity, pasture area, patch area or number of patches per pasture (Table 1), which is congruous with previous work noting the range of ecosystems in which the fire–grazing interaction has been reported (Allred, Fuhlendorf, Engle, *et al.* 2011). At the same time, the fact that heterogeneity-based management did not universally create patch contrast underscores the fundamental link between fire and grazing in pyric-herbivory.

Pyric-herbivory – the unique ecological disturbance created by the fire–grazing interaction – depends upon fire to influence grazing behaviour such that both grazing and vegetation respond to the spatial pattern of fire (Fuhlendorf *et al.* 2009). However, our results clearly indicate that the influence of fire on the pattern of grazing and vegetation in the landscape is weak unless fire and grazing function as an interacting disturbance. A universal response to pyric-herbivory requires the pattern of fire in the landscape to influence vegetation structure and grazing behaviour and create a contrast between patches that attract grazing (magnet patches) and patches that deter grazing (deterrent patches). However, the influence of fire is weak if it fails to override other environmental factors that contribute to grazer selectivity at the landscape level (Adler, Raff, & Lauenroth 2001; Allred, Fuhlendorf, & Hamilton 2011).

Grazing followed the spatial pattern of fire and created patch contrast at three of our five locations, but heterogeneity-based management failed to couple fire and grazing into an interacting disturbance at two locations. We attribute the lack of a fire–grazing interaction at Klemme and the GRG to poor fire spread in the burned patches created by a history of overgrazing at each location and invasive plant species that modified the fuelbed in the GRG. Severe grazing in years preceding fire reduces fire spread by reducing the fuel load and creating gaps in the fuelbed (Kerby, Fuhlendorf, & Engle 2007; Davies, Svejcar, & Bates 2009; Leonard, Kirkpatrick, & Marsden-Smedley 2010; Davies *et al.* 2010). At Klemme and the GRG, stocking rates prior to experimental treatment were much greater than pre-treatment stocking rates at Cooper, Stillwater and the TGPP (Table 1). Heavy grazing reduced fuel loading, which reduced fire spread. As such, subsequent grazing preference was not determined by pyric-herbivory but rather by environmental variability at spatial scales other than the burned patches– e.g., areas close to water, shade, or patches of preferred forage species (Senft *et al.* 1987; Bailey *et al.* 1996).

Overstocking contributed to reduced fuel load in the GRG, but discontinuity in the fuelbed appears to have been caused not by gaps of bare ground but by an abundance of invasive tall fescue (*Schedonorus phoenix* (Scop.) Holub). Tall fescue creates a barrier to fire spread: during the conventional prescribed burning period, live fuel moisture content in tall fescue exceeds that required to sustain fire spread (McGranahan et al. 2012). In the GRG, grazing reduced accumulated dead fuel and increased proportion of live tall fescue in the fuelbed, which thereby reduced fire spread (McGranahan 2011).

Our multivariate method for determining variance in plant functional groups accommodated functional group classifications for each location. This approach is both flexible in combining data from individual experiments into a comparative analysis and allowed for insight into the role specific plant functional groups play in the fire–grazing interaction. For example, Cooper had the greatest shrub component in the vegetation, and patch contrast at this location is likely due to the adaptation of the dominant shrub, sand sagebrush (*Artemisia filifolia* Torr.), to quickly resprout after fire (Winter *et al.* 2011). At the other end of the productivity gradient, management for heterogeneity failed to create patch contrast in the GRG, which had a much lower abundance of native plant species (Pillsbury *et al.* 2011) than the other tallgrass prairie locations, which were not only relatively free of invasive plant species but were dominated by native plants (Fuhlendorf & Engle 2004; Fuhlendorf *et al.* 2006). Given that patch contrast increases with variance in plant functional group composition (Fig. 3), native plant species with an evolutionary history of pyric-herbivory are likely important in ensuring that management for heterogeneity achieves the desired outcomes.

The long-term legacy effect of historical management as regulators of pyric-herbivory are not known, although recent data from Klemme suggest that when stocking rate is moderated, plant productivity recovers, fuel load and fuel continuity increase, and fire drives spatial pattern of grazing (Limb *et al.* 2011). For the period examined in this study, Klemme had a diverse composition of plant functional groups despite low patch contrast, which is probably due to spatially-heterogeneous grazing driven by environmental factors other than fire, because the influence of fire was small (Adler *et al.* 2001). In the GRG, however, both patch contrast and the range of plant functional group composition were slight, probably due to the great abundance of tall fescue on historically severely stocked pastures (McGranahan 2011). Thus, restoration of pyric-herbivory at Klemme probably depends primarily on the recovery of plant productivity, but recovery for overstocking and invasive species control may be required before pyric-herbivory can be fully restored to the GRG.

The five rangeland locations included here used domestic cattle *Bos taurus* as grazers, reflecting the fact that native herbivores have largely been extirpated from central North American rangelands and cattle ranching is the predominant use of many rangelands worldwide. Even in ecosystems where native herbivores persist, the natural fire regimes of many rangelands have been substantially altered. However, domestic livestock and prescribed fire can re-create the pre-historic mosaic: evidence from the North American tallgrass prairie suggests the conservation value of cattle might be analogous to that of bison *Bison bison*, the dominant native herbivore, in heterogeneous landscapes managed with fire (Towne, Hartnett, & Cochran 2005; Allred, Fuhlendorf, & Hamilton 2011). Management for heterogeneity has been shown to increase the diversity of invertebrates, small mammals, large ungulates and birds in several ecosystems worldwide (Archibald & Bond 2004; Fuhlendorf *et al.* 2006; Bouwman & Hoffman 2007; Coppedge *et al.* 2008; Engle *et al.* 2008; Fuhlendorf *et al.* 2009; Doxon *et al.* 2011). Moreover, patch burn-grazing is an agriculturally-productive management practice in working rangeland grazed by cattle (Limb *et al.* 2011).

Conclusion

Our results demonstrate that management for heterogeneity using patch burn-grazing does not universally create patch contrast in rangelands. Rather, patch burn-grazing creates patch contrast only if fire is the primary driver of grazer site selection across the landscape. The level of patch contrast appears to correspond to the level of variance in plant functional group composition. Management for heterogeneity using patch burn-grazing can increase heterogeneity in vegetation structure, and therefore increase rangeland biodiversity compared to management for homogeneity, but only when fire behaviour influences grazing behaviour.

Three important themes that apply to management for heterogeneity emerged from our findings. First, managers choosing to apply patch burn-grazing should stock livestock at a moderate stocking rate. Each location in our study that did not show patch contrast was excessively stocked before being managed with patch burn-grazing, which suggests that excessive stocking reduces fire spread and decreases the influence of fire on the spatial pattern of grazing. The second theme is that invasive species that reduce fire spread render fire ineffective to drive spatial pattern of grazing. Finally, by moderating stocking rate on overgrazed rangelands, plant productivity and fuel load will recover and fire will again influence spatial pattern of grazing (Limb *et al.* 2011). However, the extent to which invasive species persist as a barrier to effective patch burn-grazing remains unknown.

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Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1. Description of data included in rangeland heterogeneity analysis

Table 1: Precipitation, vegetation, and grazing information for five experimental locations comparing heterogeneously-applied fire management with homogeneous fire regimes. Refer to Methods and Appendix S1 for information about experimental design, data collected, and years included. Locations are listed geographically from west to east

Study location	Cooper [a]	Klemme[b]	Stillwater [c]	TGPP[d]	GRG [e]
Annual precipitation (cm)					
Long-term mean	57	78	83	88	91
Study period range	41-77	51-82	61-99	59-109	97-147
Vegetation type	Artemisia shrubland-mixed prairie	Midgrass prairie	Tallgrass prairie	Tallgrass prairie	Tallgrass prairie
Stocking rate [f]					

Prior to study period	Moderate	Heavy	Moderate	Moderate-light	Severe
Study period (Animal-Unit-Months ha^{-1})	0.8 (Moderate)	1.6 (Moderate)	4.3 (Moderate)	3.2 (Moderate-light)	3.1 (Heavy)
Grazing season	1 April - 15 Sept.	15 Mar. - 15 Sept.	1 Dec. - 1 Sept.	15 Apr. - 20 Jul.	1 May - 1 Oct.
Pasture area (ha)	406-848	ca. 50	45-65	400-900	15 - 31
Annual primary productivity [g] (kg ha^{-1})	1500	2000	5600	6000	6700

[a]Hal and Fern Cooper Wildlife Management Area. (Gillen & Sims 2004; Winter *et al.* 2012)

[b] Marvin Klemme Experimental Research Range. (Gillen, Eckroat, & McCollum 2000; Limb *et al.* 2011)

[c] Stillwater Research Range. (Gillen, Rollins, & Stritzke 1987; Fuhlendorf & Engle 2004; Limb *et al.* 2011; OK Mesonet

2011)

[d] Tallgrass Prairie Preserve. (Hamilton 2007; Coppedge *et al.* 2008; OK Mesonet 2011)

[e] Grand River Grasslands. (IEM 2011; Pillsbury *et al.* 2011)

[f]Stocking rate categories expressed in relation to local recommendations from the USDA Natural Resource Conservation Service.

[g] Estimated annual primary productivity of native vegetation not recently disturbed by grazing or fertilization. Published data were used for Cooper (Gillen & Sims 2004), Klemme (Gillen, Eckroat, & McCollum 2000), and Stillwater (Gillen, Rollins, & Stritzke 1987). Unpublished data on end-of-season biomass one year after fire from at least one year within the study period included here were used to estimate annual primary productivity at the TGPP and the GRG.

Figure 1: Proportion of total variance in vegetation structure contributed by the patch term in nested, spatially hierarchical sampling measures patch contrast at five experiments comparing management for heterogeneity (blue triangles) to management for homogeneity (orange circles). Data are plotted for each pasture replicate within each of the five locations. Locations are arranged along a general west-to-east geographical gradient (western Oklahoma – south-central Iowa), which corresponds to a precipitation gradient. Asterisks represent results of Student's t tests for differences in means of management groups: " ** " $P < 0.01$; " * " $P \leq 0.05$.

Figure 2: Range of RDA1 scores measures variance in plant functional group composition at five experiments comparing management for heterogeneity (blue triangles) to management for homogeneity (orange circles). Data are plotted for each pasture replicate within each of the five locations. Locations are arranged along a general west-to-east geographical gradient (western Oklahoma – south-central Iowa), which corresponds to a precipitation gradient. Asterisks represent results of Student's t tests for differences in means of management groups: " * " $P \leq 0.05$.

Figure 3: Effect size of patch contrast (Y axis) plotted against effect size of variance in plant functional group composition (X axis), with corresponding 95% confidence intervals, for five rangeland experiments comparing management for heterogeneity against management for homogeneity. Effect sizes are calculated with the meta-analysis statistic Cohen's d (see Methods for equation) and are plotted on a log scale.

Fig. 1

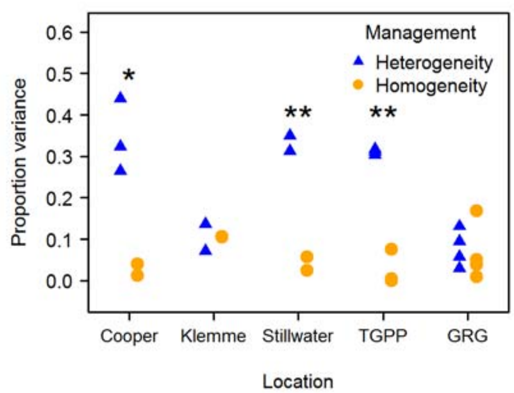

Management
Heterogeneity
Homogeneity
Proportion variance
0.0
0.1
0.2
0.3
0.4
0.5
0.6
*
**
**
Cooper
Klemme
Stillwater
TGPP
GRG
Location

Fig. 2

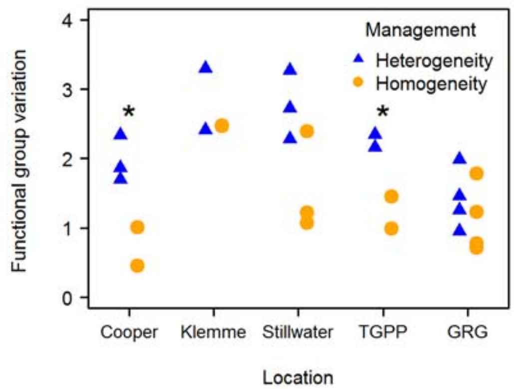
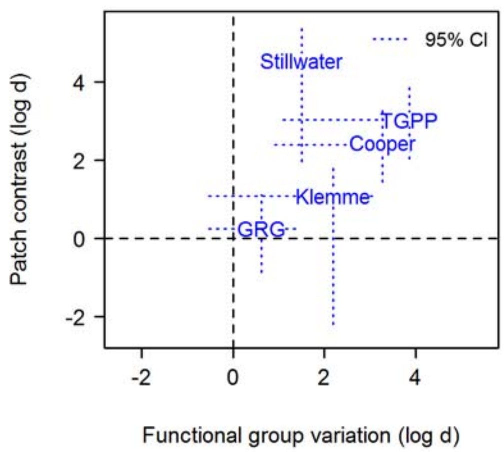

Management
Heterogeneity
Homogeneity
Functional group variation
0
1
2
3
4
*
*
Cooper
Klemme
Stillwater
TGPP
GRG
Location

Fig. 3


95% CI
Stillwater
TGPP
Cooper
Klemme
GRG
Patch contrast (log d)
4
2
0
-2
-2
0
2
4
Functional group variation (log d)